

## Comparative Primate Energetics and Hominid Evolution

WILLIAM R. LEONARD AND MARCIA L. ROBERTSON  
*Department of Anthropology, University of Florida,  
Gainesville, Florida 32611*

**KEY WORDS** energy metabolism; ecosystem ecology; foraging behavior; diet quality; activity patterns; *Homo erectus*

**ABSTRACT** There is currently great interest in developing ecological models for investigating human evolution. Yet little attention has been given to energetics, one of the cornerstones of modern ecosystem ecology. This paper examines the ecological correlates of variation in metabolic requirements among extant primate species, and uses this information to draw inferences about the changes in energy demands over the course of human evolution. Data on body size, resting metabolism, and activity budgets for selected anthropoid species and human hunter-gatherers are used to estimate total energy expenditure (TEE). Analyses indicate that relative energy expenditure levels and day ranges are positively correlated with diet quality; that is, more active species tend to consume more energy-rich diets. Human foragers fall at the positive extremes for modern primates in having high expenditure levels, large ranges, and very high quality diets. During hominid evolution, it appears that TEE increased substantially with the emergence of *Homo erectus*. This increase is partly attributable to larger body size as well as likely increases in day range and activity level. Assuming similar activity budgets for all early hominid species, estimated TEE for *H. erectus* is 40–45% greater than for the australopithecines. If, however, it is assumed that the evolution of early *Homo* was also associated with a shift to a more “human-like” foraging strategy, estimated expenditure levels for *H. erectus* are 80–85% greater than in the australopithecines. Changing patterns of resource distribution associated with the expansion of African savannas between 2.5 and 1.5 mya may have been the impetus for a shift in foraging behavior among early members of the genus *Homo*. Such ecological changes likely would have made animal foods a more attractive resource. Moreover, greater use of animal foods and the resulting higher quality diet would have been important for supporting the larger day ranges and greater energy requirements that appear to have been associated with the evolution of a human-like hunting and gathering strategy. *Am J Phys Anthropol* 102:265–281, 1997 © 1997 Wiley-Liss, Inc.

Human paleontologists have become increasingly interested in framing the study of hominid evolution in an ecological perspective. Several recent studies, for example, have suggested that major trends in human evolution were precipitated by large-scale ecosystem changes (e.g., Rogers et al., 1994; Vrba, 1988, 1993). In light of this growing interest in hominid ecology, it is surprising that little attention has been given to energy

dynamics. Research on bioenergetics, the biological transfer and utilization of energy, is a central component of ecosystem ecology (e.g., E.P. Odum, 1971; H.T. Odum, 1971;

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\*Correspondence to: William R. Leonard, Department of Anthropology, 1350 Turlington Hall, University of Florida, Gainesville, FL 32611-7305.

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Begon et al., 1990). Such work examines how individuals and populations extract energy from their environment, and how, in turn, that energy is allocated for biological processes such as maintenance, activity, growth, and reproduction. Studies of energy flow help to provide insights into how the availability and distribution of nutrient energy in an ecosystem may influence such parameters as population density and growth rates for a particular species (H.T. Odum, 1971; Begon et al., 1990).

An understanding of energy dynamics is ultimately dependent upon quantifying individual and population-level energy demands. Total daily energy requirements of a healthy organism are determined by such factors as body size (a correlate of resting metabolic requirements), activity, growth, and reproductive status. Over the course of hominid evolution it appears that there were changes in all four of these parameters. Body size has increased markedly since the emergence of hominids some 4 million years ago, as evidenced by the fossil remains of *Australopithecus* and early *Homo* (McHenry, 1992a,b, 1994). Similarly, activity costs, particularly those associated with foraging, are likely to have changed as our ancestors began to exploit their environment in new ways. Finally, the evolution of our species' prolonged growth period and distinctive reproductive pattern (i.e., birth of altricial young) also has had important metabolic implications (Holliday, 1986; Leonard and Robertson, 1992; Rivers, 1988; Webster, 1988).

Researchers in both human and primate ecology have used a variety of different approaches for quantifying energy requirements (e.g., Coelho et al., 1976, 1979; Dasilva, 1992; Nagy and Milton, 1979 [non-human primates]; James and Schofield, 1990; Leonard et al., 1995; Leslie et al., 1984; Norgan et al., 1974; Schulz and Schoeller, 1994; Thomas, 1973; Ulijaszek, 1995 [humans]). Such methods, however, have not as yet been standardized or broadly applied to contemporary primate species or early hominids. Thus, the purpose of this paper is threefold: first, to develop a comparable method for quantifying inter-specific variation in total daily energy requirements among extant primate species; second, to

examine how total energy expenditure (TEE) among extant primates varies with body size and feeding strategy; and finally, to utilize the patterns of variation among extant primates to draw inferences about changes in TEE over the course of hominid evolution. Previous studies have examined the energy costs associated with increased brain size in human evolution (see Aeillo and Wheeler, 1995; Leonard and Robertson, 1992, 1994, 1996). In contrast, the present study will examine likely changes in *total* energy expenditure, as influenced by changes in body size and activity patterns. This paper, then represents a first step in understanding hominid evolution from the perspective of ecological energetics.

## MATERIALS AND METHODS

### Primate and human ecological data

Data on activity budgets, day ranges, body weights, and dietary consumption of 17 non-human primate species and two modern human foraging groups were compiled from the literature and are presented in Tables 1 and 2. The nonhuman primate data include nine New World monkey species: *Aotus trivirgatus* (Wright, 1978), *Alouatta palliata* (Milton, 1980; Smith, 1977), *Ateles geoffroyi* (Klein and Klein, 1977), *Cebus apella*, *Cebus albifrons*, *Callicebus moloch*, *Saguinus fuscicollis*, *Saguinus imperator*, and *Saimiri sciureus* (Terborgh, 1983); four Old World Monkeys: *Cercocebus albigena* (Waser, 1977), *Colobus guereza* (Oates, 1977), *Macaca fascicularis* (Temerin et al., 1984) and *Papio anubis* (Eley et al., 1989; Jolly, 1972; Richard, 1985); and four ape species: *Hylobates lar* (Raemaekers, 1979), *Pan troglodytes* (Rodman, 1984; Rodman and McHenry, 1980; Wrangham, 1977) *Pongo pygmaeus* (Rodman, 1977, 1984), and *Symphalangus syndactylus* (Raemaekers, 1979). Data for human hunter-gatherers were derived from the works of Lee (1968, 1979) on the !Kung San of Botswana and Hill and colleagues (1984, 1985; Hurtado et al., 1985) on the Ache of Paraguay.

Diet quality (DQ) for each of the species was measured using an index developed by Sailer et al. (1985). This index is based on a weighting of the percentages, by weight or feeding time, of structural plant material (e.g., leaves, bark), reproductive plant parts

TABLE 1. Body weight, activity budgets, day range, and diet quality in 17 extant anthropoid species<sup>1</sup>

Species	Sex	Weight (kg)	Activity budgets (hr/day)					Range (kg)	Diet quality
			Sleep	Rest	Feed	Locomotion	Other		
Ceboidea									
<i>A. palliata</i>	M	8.50	12.00	8.64	2.04	.84	.48	.40	136.0
	F	6.40	12.00	8.64	2.40	.60	.36	.30	136.0
<i>A. trivirgatus</i>	M/F	0.85	11.88	2.67	6.42	2.54	.49	.25	177.5
<i>A. geoffroyi</i>	M/F	8.41	12.00	7.56	2.66	1.78	.00	1.00	200.0
<i>C. moloch</i>	M/F	0.70	12.00	6.48	3.12	2.28	.12	.96	198.0
<i>C. apella</i>	M/F	2.60	12.00	1.44	7.92	2.52	.12	2.07	314.0
<i>C. albifrons</i>	M/F	2.40	12.00	2.16	7.32	2.52	.00	1.82	296.0
<i>S. imperator</i>	M/F	0.40	12.00	3.00	6.12	2.52	.36	1.42	287.0
<i>S. fuscicollis</i>	M/F	0.30	12.00	5.28	3.84	2.40	.48	1.22	287.0
<i>S. sciureus</i>	M/F	0.80	12.00	1.32	7.32	3.24	.12	2.00	323.0
Cercopithecoidea									
<i>C. albigena</i>	M/F	7.90	12.00	4.34	5.10	2.56	.00	1.11	234.0
<i>C. guereza</i>	M/F	7.00	12.00	8.09	1.20	1.95	.76	.54	126.0
<i>M. fascicularis</i>	M/F	5.50	12.63	4.55	1.59	5.23	.00	1.90	200.0
<i>P. anubis</i>	M	29.30	12.83	1.41	5.16	3.62	.98	4.60	207.0
	F	13.00	12.70	.75	6.29	3.24	1.02	4.10	207.0
Hominoidea									
<i>H. lar</i>	M/F	6.00	15.40	2.20	3.60	2.80	.00	.74	181.0
<i>P. troglodytes</i>	M	39.50	12.79	2.14	6.68	1.65	.74	4.80	178.0
	F	29.80	12.79	2.14	7.28	1.05	.74	3.00	178.0
<i>P. pygmaeus</i>	M	83.60	12.73	3.67	6.43	1.05	.12	.30	163.0
	F	37.80	12.73	5.04	4.54	1.36	.33	.30	174.5
<i>S. syndactylus</i>	M/F	10.50	13.60	2.90	5.20	2.30	.00	1.49	167.0

<sup>1</sup>See text for sources of data.TABLE 2. Body weight, activity budgets, day range, and diet quality in two human foraging societies<sup>1</sup>

Group	Sex	Weight (kg)	Activity budgets (hr/day)							Range (km)	Diet quality
			Sleep	Sit	Stand	Walk	Light work	Moderate work	Heavy work		
!Kung	M	46.0	10.0	6.5	1.0	2.5	2.5	1.0	0.5	14.9	255.5
	F	41.0	10.0	6.5	1.5	2.5	3.0	0.5	0.0	9.1	255.5
Ache	M	59.6	12.5	2.0	0.3	4.0	2.8	0.6	1.8	19.2	263.0
	F	51.8	12.2	3.9	0.4	1.9	3.6	2.0	0.0	9.2	263.0

<sup>1</sup> Sources of data listed in the text.

(e.g., fruit), and animal material (including insects) in the diet:

$$DQ = 3.5(a) + 2(r) + s \quad (1)$$

where:

a = percent of diet derived

from animal material

r = percent of diet derived

from reproductive plant parts

s = percent of diet derived

from structural plant parts.

Hence, with this index, DQ ranges from a minimum of 100 (i.e., a diet of 100% foliage) to a maximum of 350 (100% animal material). This index is superior to such commonly used measures as "percent foliage,"

because it captures more of the variation in primate diets.

### Metabolic data

Experimental data on resting metabolic rates (RMR) were obtained for 11 of the 18 primate species (including humans) noted above: *A. palliata* (Milton et al., 1979), *A. trivirgatus* (Goffart, 1977), *S. sciureus* (Le Maho et al., 1981), *Cercocebus spp.* (Bruhn, 1934), *C. guereza* (Müller et al., 1983), *M. fascicularis* (Tokura et al., 1975), *P. papio* (Proppe and Gale, 1970; Bruhn, 1934; Hohimer and Smith, 1979), *H. lar* (Bruhn, 1934), *P. pygmaeus* (Bruhn, 1934), *P. troglodytes* (Bruhn, 1934), and *H. sapiens* (Schofield, 1985). Where necessary, metabolic rate units were converted from liters of O<sub>2</sub> to

kcal, assuming a respiratory quotient (RQ) of 0.9. At this RQ, each liter of oxygen consumed is equal to 4.92 kcal (McArdle et al., 1986).

### Fossil hominid data

Sex-specific estimates of body size in various fossil hominid species were taken from McHenry (1992a,b) and Ruff and Walker (1993). These estimates were derived from measurements of hindlimb joint size, based on regression equations developed on a sample of modern humans.

## RESULTS AND DISCUSSION

### Estimation of energy requirements in extant primate species

As noted in the introduction, total metabolic requirements of an individual are dependent upon a number of different physiological parameters (i.e., body size, activity patterns, growth, and reproductive status). The model developed below will consider only the two *central* determinants of total energy needs: (1) resting metabolic requirements and (2) metabolic requirements for activity.<sup>1</sup> Thus, the estimates generated from this model will reflect the caloric needs of adult, non-pregnant/non-lactating individuals of each species considered.

**Resting metabolism.** Resting metabolic rate denotes the amount of energy utilized by an inactive organism under thermoneutral conditions (Durnin and Passmore, 1967). Numerous studies have demonstrated that across a diverse number of animal species RMR scales to the three-quarters power of body weight (Brody, 1945; Kleiber, 1932). Specifically, the Kleiber (1961) equation predicts an animal's resting energy requirements (kcal/d) as:

$$\text{RMR} = 70 \cdot \text{Wt}^{0.75} \quad (2)$$

where:

RMR = Resting metabolic requirements (kcal/d)

Wt = Body weight (kg).

Previous work has shown that anthropoid primates, as a group, do not significantly depart from the so-called Kleiber scaling relationship (Kurland and Pearson, 1986; Leonard and Robertson, 1994, 1996). This result is somewhat surprising given the large brain-body mass ratios of anthropoids, coupled with the high metabolic costs of the brain (Holliday, 1986; Kety, 1957; Mink et al., 1981).

Figure 1 presents the allometric relationship between RMR (kcal/day) and body weight (kg) for humans and 10 other anthropoid species. The regression that best fits these  $\log_{10}$ -transformed data has a slope of 0.761:

$$\text{RMR} = 69.1 \cdot \text{Wt}^{0.761} \quad (3)$$

The 95% confidence limits for the slope (0.68–0.84) easily accommodate that of the Kleiber equation (0.75). Consequently, large-brained anthropoids, as a group, do not depart from the general interspecific allometric relationship between metabolism and body size; rather they expend a significantly larger proportion of their metabolic energy to “feed their brains” (Leonard and Robertson, 1992, 1994; Mink et al., 1981).<sup>2</sup>

A few of these species do, however, have RMRs that deviate markedly from predicted levels. Metabolic rates of the night (*A. trivirgatus*) and the colobus (*C. guereza*) monkeys fall below those predicted by the Kleiber equation by 26 and 12%, respectively. The crab-eating macaque, on the other hand, has a resting metabolic rate that is 36% above its predicted level.

**Activity patterns.** The other principal determinant of an animal's total energy requirements is the amount of activity or work performed during the course of the day. Energy expenditure on activities is highly variable across animal species (see Nagy, 1987; Peterson et al., 1990). To evaluate the variability in total energy expenditure among primates, detailed activity budgets were obtained for 17 anthropoid species and

<sup>1</sup>The model developed here can be modified to incorporate growth and reproductive parameters (see Leslie et al., 1984). These, however, are beyond the scope of the present paper and will be addressed in future publications.

<sup>2</sup>The RMR vs. weight relationship presented here does not significantly differ from that previously demonstrated on a larger sample ( $n = 20$ ) of anthropoid primates by Leonard and Robertson (1992).

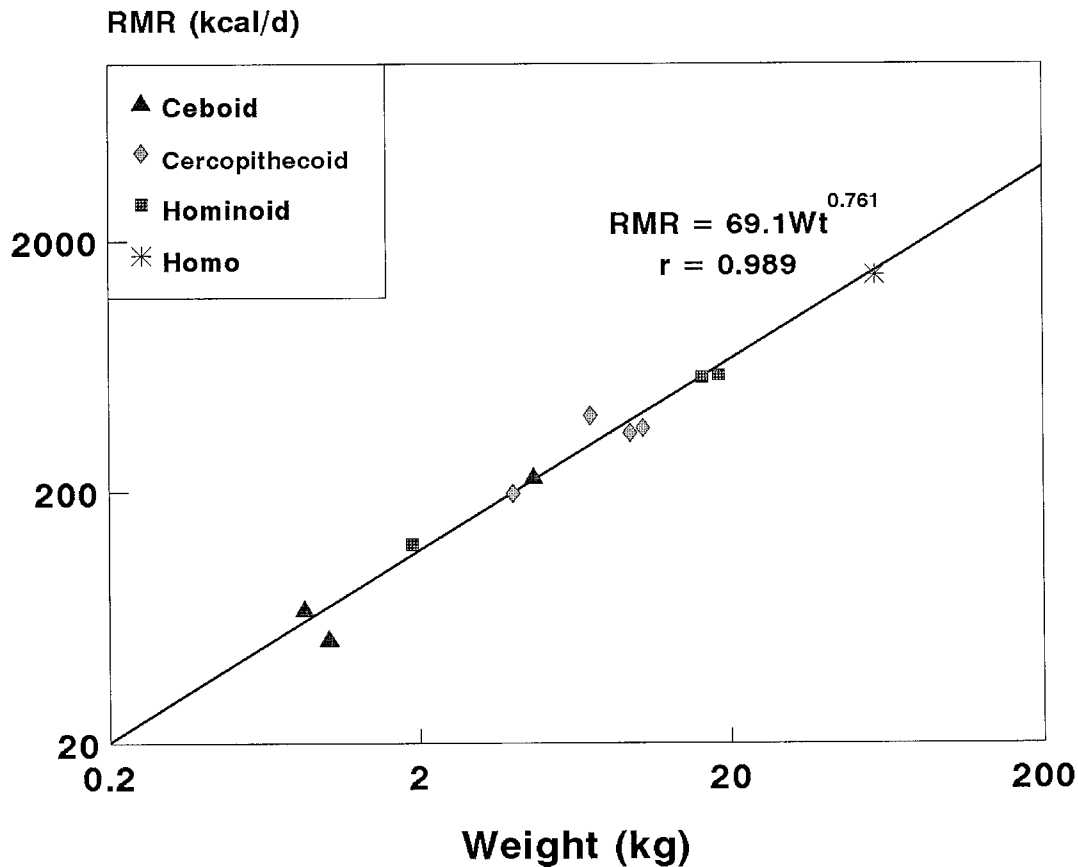


Fig. 1. Log-log plot of resting metabolic requirements (RMR; kcal/day) vs. body weight (kg) for 11 primate species. The allometric relationship between RMR and weight for primates ( $RMR = 69.1 \cdot Wt^{0.761}$ ;

$r = 0.989$ ) is not significantly different from the Kleiber relationship ( $RMR = 70 \cdot Wt^{0.750}$ ) for mammals in general.

two groups of modern human hunters and gatherers. These activity data were converted into caloric costs using energetics models developed by Coelho and colleagues (Coelho, 1974; Coelho et al., 1976) for nonhuman primates and World Health Organization (FAO/WHO/UNU, 1985) for humans.

Table 1 presents the data on (1) body weights (in the wild), (2) activity patterns, (3) day range (km), and (4) diet quality for the 17 nonhuman primate species. Sex-specific data are provided for those species with high body size and/or behavioral dimorphism. Activities are divided into five categories: (1) inactive (sleeping or dormant), (2) resting, (3) feeding, (4) locomotion, and (5) other (e.g., socializing, grooming), and are quantified as hours/day. The energetic costs

of these various primate activities (expressed as multiples of RMR) are listed in Table 3 and have been adapted from data presented by Coelho and co-workers (Coelho, 1974; Coelho et al., 1976, 1979).

The present model departs from Coelho's estimates of locomotion using the empirical equations developed by Taylor and colleagues (1970; Taylor and Rowntree, 1973) rather than those of Tucker (1970) (see Table 3). The Taylor equations appear to provide a more realistic way of estimating energy expenditure in the wild since the Tucker equations reflect *minimum costs* of locomotion (in terms of kcal/distance travelled) that are achieved only at very rapid speeds (Taylor et al., 1973). Hence, the estimates of energy expenditure for movement are systemati-

TABLE 3. Energetic costs of selected primate activities<sup>1</sup>

Activity	Energy constant [K <sub>i</sub> ] <sup>2</sup> (multiples of RMR)
Sleeping (RMR)	1.00
Resting	1.25
Feeding	1.38
Socialize/play	2.35
Hang/bridge	5.00
Locomotion <sup>3</sup>	—

<sup>1</sup> Values adapted from Coelho (1974) and Coelho et al. (1976), except where otherwise noted.

<sup>2</sup> From the presented values, caloric costs for individual activities (except locomotion) can be calculated as follows:

$$C_i = K_i(\text{RMR})T_i/24$$

where:

C<sub>i</sub> = Energy Cost (kcal) for an individual activity "i"  
K<sub>i</sub> = Energetic constants for each activity "i" (see table)  
T<sub>i</sub> = Time (hours) spent in some activity "i."

<sup>3</sup> Costs for quadrupedal locomotion (C<sub>loc</sub>) were calculated by modifying the equations presented by Taylor et al. (1970):

$$C_{\text{loc}} = (0.041\text{Wt}^{0.60})\text{DR} + (0.029\text{Wt}^{0.75})T_{\text{loc}}$$

where:

C<sub>loc</sub> = Energy cost (kcal) of locomotion  
Wt = Weight (in grams)  
T<sub>loc</sub> = Time (hrs) spent in locomotion  
DR = Day range (km).

cally *higher* than those of Coelho and co-workers.

Energy expenditure for two modern human foraging groups (the !Kung and Ache) was calculated in a similar manner. Table 2 presents body weight, activity and dietary data for the !Kung and Ache, separated by sex. Daily activities were grouped according to the energetic categories presented in FAO/WHO/UNU (1985) and James and Schofield (1990): (1) sleeping/lying, (2) sitting, (3) standing, (4) walking, (5) light work (e.g., weaving, sweeping), (6) moderate work (e.g., digging, ploughing), and (7) heavy work (e.g., chopping, felling trees). As with the nonhuman primate data, these categories reflect expenditure levels as a multiple of resting metabolism (see Table 4). For example, energy costs for lying and sleeping equal RMR, whereas "heavy work" activities require 5.5 times resting needs. The cost of locomotion was calculated assuming a normal human walking speed of 4.5 km/hr. At this speed, bipedalism is less energetically expensive than quadrupedal locomotion (see Rodman and McHenry, 1980; Leonard and Robertson, 1995).

**Total energy expenditure.** Total energy expenditure (kcal/d) was determined by adding the caloric needs for maintenance (i.e., needs when sleeping or dormant) to those

TABLE 4. Energetic costs for selected human activities<sup>1</sup>

Activity	Energy constant [K <sub>i</sub> ] <sup>3</sup> (multiples of RMR)
Sleeping/lying (RMR) <sup>2</sup>	1.00
Sitting	1.20
Standing	1.40
Walking	3.60
Light work (e.g., cooking)	2.20
Moderate work (e.g., digging)	3.80
Heavy work (e.g., tree felling)	5.50

<sup>1</sup> Adapted from James and Schofield (1990).

<sup>2</sup> RMRs are calculated from the sex-specific equations for individuals 18–30 years presented in the 1985 FAO/WHO/UNU energy and protein recommendations: Males: RMR = 15.3(Wt) + 679; females: RMR = 14.7(Wt) + 496.

<sup>3</sup> From the presented values, caloric costs for individual activities can be calculated as follows:

$$C_i = K_i(\text{RMR})T_i/24$$

where:

C<sub>i</sub> = Energy Cost (kcal) for an individual activity "i"  
K<sub>i</sub> = Energetic constants for each activity "i" (see table)  
T<sub>i</sub> = Time (hours) spent in some activity "i."

needed for all daily activities. Thus, for both the human foragers and nonhuman primate species, TEE for a typical day can be expressed as the sum caloric costs for maintenance and for all individual activities:

$$\text{TEE} = \sum_{i=1}^n C_i \quad (4)$$

where:

TEE = Total energy expenditure (kcal/d)

C<sub>i</sub> = Energy costs (kcal) associated  
with individual activities "i"  
(see Table 3 for primates and  
Table 4 for humans).

Resting metabolic rates were calculated based on data from direct measurements (from Fig. 1), adjusting for differences in body weight between individuals living under laboratory and natural conditions. For those species in which metabolic data were not available, RMR was estimated using the Kleiber equation. Similarly, the energetic cost for each individual activity is determined based on the amount of time spent in that activity (from Tables 1 and 2) and the metabolic intensity of that activity (from Tables 3 and 4).

The values generated by the above models should be considered *minimum estimates* of TEE since (1) energetic costs of thermoregulation, digestion of food, or reproduction are not considered, (2) behavioral observations

TABLE 5. Body weight and levels of energy expenditure in selected anthropoid species and human foragers

Species	Sex	Weight (kg)	RMR (kcal/d)	TEE (kcal/d)
<b>Ceboidea</b>				
<i>A. palliata</i>	M	8.50	363	428
	F	6.40	293	343
<i>A. trivirgatus</i>	M/F	.85	46	60
<i>A. geoffroyi</i>	M/F	8.41	346	415
<i>C. moloch</i>	M/F	.70	54	66
<i>C. apella</i>	M/F	2.60	143	185
<i>C. albifrons</i>	M/F	2.40	135	172
<i>S. imperator</i>	M/F	.40	35	45
<i>S. fuscicollis</i>	M/F	.30	28	38
<i>S. sciureus</i>	M/F	.80	66	84
<b>Cercopithecoidea</b>				
<i>C. albigena</i>	M/F	7.90	327	428
<i>C. guereza</i>	M/F	7.00	265	329
<i>M. fascicularis</i>	M/F	5.50	331	393
<i>P. anubis</i>	M	29.30	956	1,281
	F	13.00	520	699
<b>Homioidea</b>				
<i>H. lar</i>	M/F	6.00	292	342
<i>P. troglodytes</i>	M	39.50	1,036	1,510
	F	29.80	839	1,144
<i>P. pygmaeus</i>	M	83.60	1,948	2,599
	F	37.80	1,074	1,499
<i>S. syndactylus</i>	M/F	10.50	408	500
<b><i>H. sapiens</i> (foragers)</b>				
!Kung	M	46.0	1,383	2,319
	F	41.0	1,099	1,712
Ache	M	59.6	1,591	3,186
	F	51.8	1,394	2,085

tend to underestimate total activity time, and (3) the energetic costs for both bipedal and quadrupedal locomotion are based on laboratory rather than field measurements. Indeed, recent studies have demonstrated that behavioral observations (the "factorial method") may systematically underestimate TEE in both humans and nonhuman primates relative to more accurate methods, such as the doubly-labelled water technique (see Nagy and Milton, 1979; Roberts et al., 1991; Haggarty et al., 1994). Nevertheless, despite these limitations the present estimates can at least provide a *relative* assessment of variation in energy expenditure across the primate order and the ecological correlates of such variation.

#### Correlates of variation in energy needs in extant primates

**TEE and body weight.** Table 5 presents the estimates of energy expenditure for each of the primate species and human groups. The log-log plot of TEE vs. body weight for each of the species is presented in Figure 2.

Total energy expenditure is strongly correlated with body mass ( $r = 0.995$ ); however, it does not scale with body weight in the same manner as RMR. The relationship between TEE and body mass is:

$$TEE = 86.0 \cdot Wt^{0.792}. \quad (5)$$

The 95% confidence limits of the scaling exponent, 0.753–0.831, do not include 0.750, and thus suggest that TEE scales at a different rate to body weight than resting metabolism.

Similar results have been reported by Nagy (1987) for a sample of 23 species of eutherian mammals. Using estimates obtained from the doubly labelled water method, he found that TEE scaled to the 0.81 power of body mass, significantly different from the scaling factor for RMR. These results indicate that TEE is not a constant multiple of RMR across mammalian species of greatly different body weights. Rather, larger mammals (including primates), on average, tend to have relatively higher energy costs above resting levels than smaller mammals.

As noted with RMR, important deviations exist between predicted and observed TEE. The magnitude of these deviations were quantified as standardized residuals (z-scores) from the least-squared regression of log-TEE vs. log-weight. Positive z-scores reflect TEEs above predicted levels, while negative scores indicate lower than expected expenditures. Figure 3 shows that human hunter-gatherers have substantially higher expenditure levels than predicted for their body size. These human groups have an average z-score of +1.54, significantly greater ( $P < 0.05$ ) than the -0.06 for ceboids, -0.07 for cercopithecoids, and -0.56 for hominoids. Thus, despite the fact that bipedalism is a more energetically efficient mode of locomotion than quadrupedalism, human foragers appear to have markedly higher energy requirements than would be expected for a primate of our size.

**TEE and diet quality.** Previous work in primate and mammalian ecology has suggested that diet quality is correlated with daily activity patterns and energy requirements. In most environments, high quality

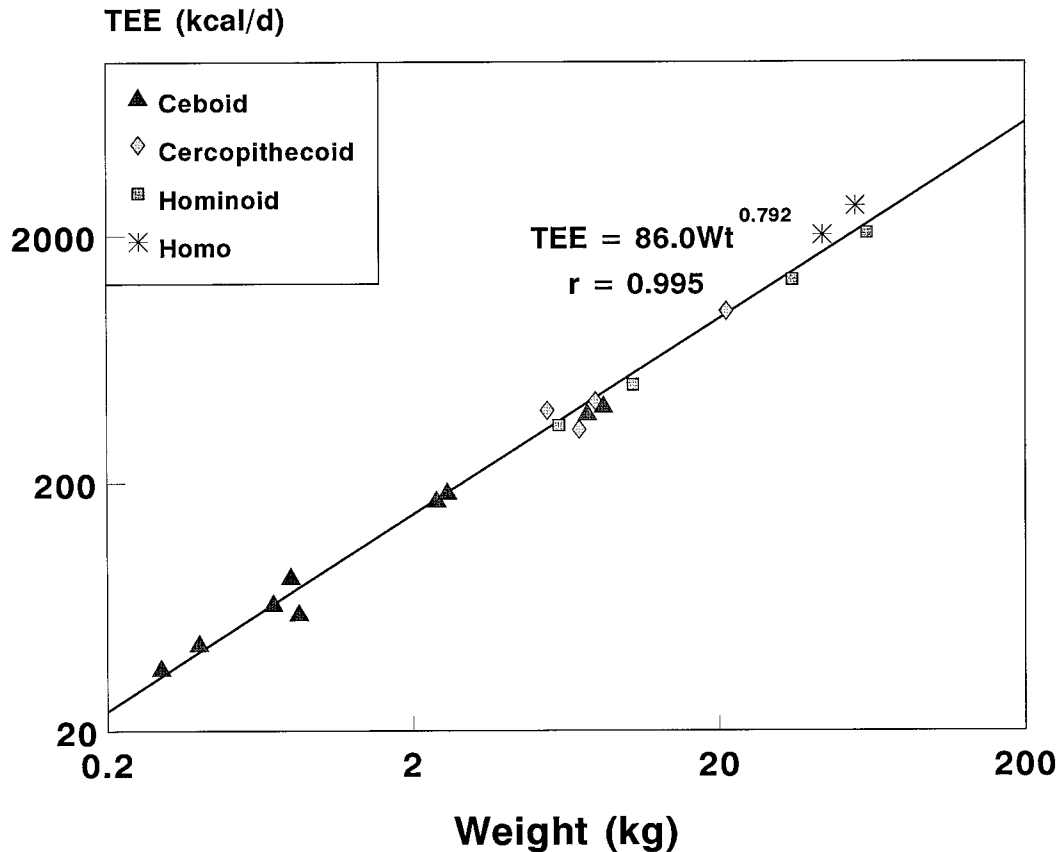


Fig. 2. Log-log plot of total energy expenditure (TEE; kcal/d) vs. body weight (kg) for 17 non-human primate species, and 2 human foraging populations. The relation-

ship between TEE and weight is  $86.0 \cdot Wt^{0.792}$  ( $r = 0.995$ ). The scaling coefficient for this relationship is significantly greater than the Kleiber exponent (0.750).

food items (i.e., fruits, seeds, insects) are less abundant and more dispersed than lower quality resources (Gaulin, 1979). This means that species subsisting on low quality foods such as leaves and bark should have small ranges and low activity budgets, while those exploiting higher quality foods should move over larger areas (Clutton-Brock and Harvey, 1977; Milton and May, 1976). Milton (1980, 1993) cites the howler monkey (*A. palliata*) as an example of a species adapting to its low quality, folivorous diet by having a relatively low activity budget. Similarly, Nagy (1987) found that herbivorous mammals had significantly lower total energy requirements than non-herbivores.

To test whether a similar association between dietary strategies and metabolic requirements occurs within primates, product-

moment correlations were determined for relative DQ vs. relative energy expenditure. Since it has been demonstrated among primates that DQ is negatively related to body size (see Gaulin, 1979; Leonard and Robertson, 1994; Sailer et al., 1985), relative DQ was measured as standardized residuals from DQ vs. log-weight regression. Similarly, relative energy expenditure was assessed as the standardized residuals from the log-TEE vs. log-weight regression (see Fig. 3).

As shown in Figure 4, relative DQ is strongly positively correlated with relative energy expenditure. This association holds for the entire sample ( $r = 0.724$ ;  $P < 0.001$ ), as well as the nonhuman primate sample alone ( $r = 0.628$ ;  $P < 0.005$ ). Similarly, residuals from the log-day range vs. log-



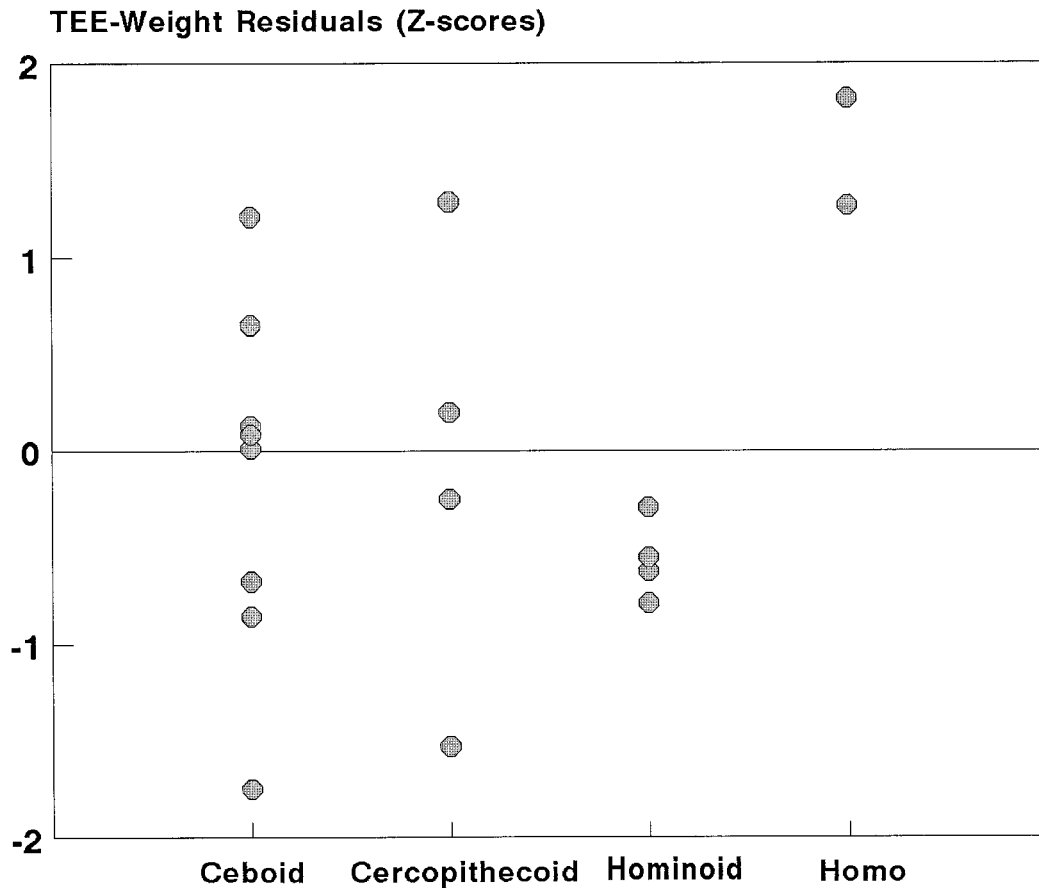


Fig. 3. Standardized residuals (z-scores) from the log-TEE vs. log-Wt regression shown in Figure 2. Human foragers have much higher energy expenditure

levels than predicted for their size ( $z = +1.54$ ). Average deviations for ceboids, cercopithecoids, and hominoids are  $-0.06$ ,  $-0.07$ , and  $-0.56$ , respectively.

weight regression are also significantly correlated with relative DQ ( $r = 0.750$ ;  $P < 0.001$ ). These results imply that among primates, relatively high activity budgets are associated with higher quality, more energy rich diets. Thus, largely folivorous species, like the howler and colobus (*C. guereza*) monkeys, tend to have relatively small day ranges and low expenditure levels. The crab-eating macaque (*M. fascicularis*), on the other hand, is a highly active species that has a relatively energy-rich diet (i.e., high in fruit and/or animal material, little or no foliage).

Human foragers conform to these trends since they are widely ranging and have diets that are quite calorically dense. Average day ranges for the !Kung and Ache are 10–20 km

(see Table 2), substantially higher than those of most other primate species. Similarly, both the !Kung and Ache exclude low quality fibrous and leafy foods from their diets. The !Kung derive a third of their energy from meat, and another 59% from mongongo nuts (Lee, 1968), whereas the Ache get over half their calories from meat (56%) and an additional 18% from honey (Hill and Hurtado, 1989).

These analyses support our general expectations about the relationships between energy expenditure, foraging range, and quality of the diet. Also, these data imply that the evolution of a hunting and gathering foraging strategy may have been associated with a substantial increase in individual and populational energy requirements. This

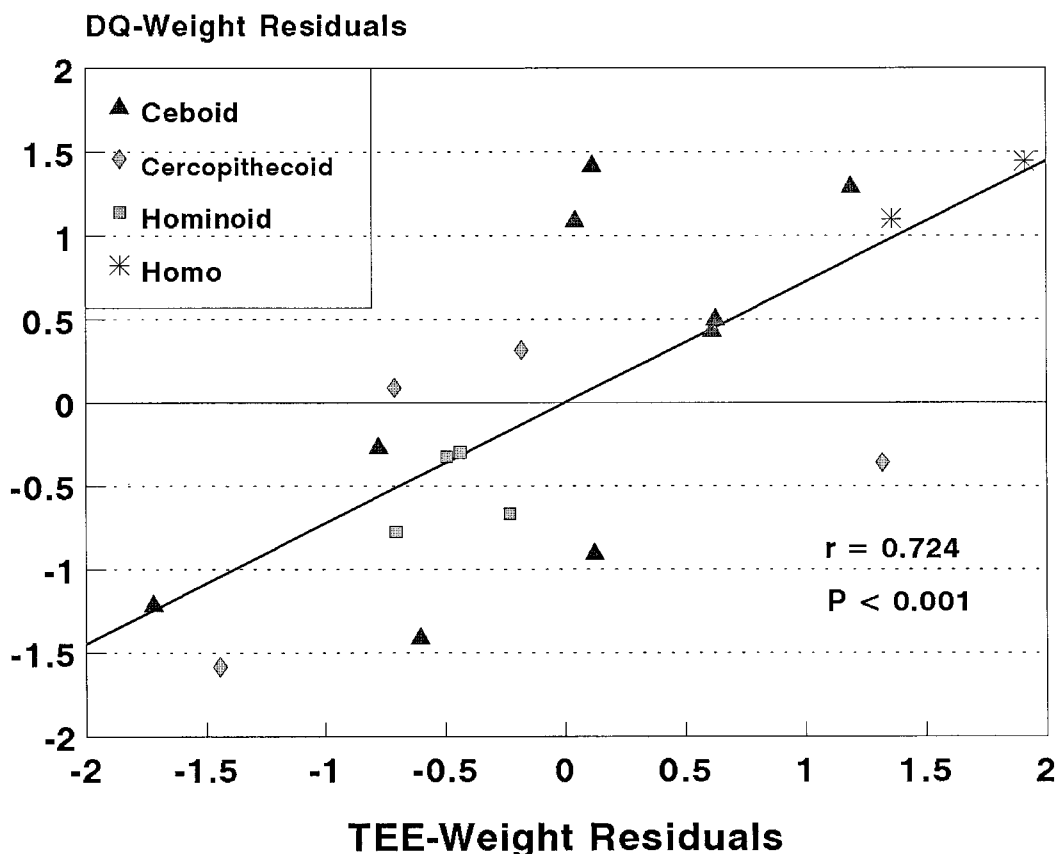


Fig. 4. Plot of relative diet quality (DQ) vs. relative energy expenditure among extant primates and human foragers. Relative DQ values are standardized residuals from the DQ-log weight regression; similarly relative energy expenditure values are the standardized residuals from the log-TEE vs. log-weight regression (pre-

sented in Fig. 3). Relative DQ is positively correlated with the energy expenditure residuals ( $r = 0.724$ ,  $P < 0.001$ , for entire sample [ $n = 19$ ];  $r = 0.628$ ,  $P < 0.005$ , for non-human primates only [ $n = 17$ ]). Human foragers display high energy demands as well as a high quality diet.

latter point will be explored in the next section.

#### Modelling hominid energetics

The models and the comparative data presented above provide a framework for estimating changes in energy requirements throughout hominid evolution. By using recent estimates of early hominid body size in conjunction with alternative assumptions about evolutionary changes in ranging and foraging behavior, we can gain insights into the potential patterns of change in energy demands during human evolution. Such estimates provide a useful first step in modelling changes in the energetic relationship between hominid populations and their eco-

systems. Additionally, the associations demonstrated between energy expenditure and diet quality in contemporary primate species have direct implications for understanding changes in patterns of resource use among early hominids.

**Body size and RMR.** From the available fossil evidence, it appears that body size has increased substantially during hominid evolution (Table 6). The most recent estimates suggest that all of the australopithecine species were relatively small-bodied. Males of *A. afarensis*, *africanus*, *robustus*, and *boisei* are all thought to be between 40 and 48 kg in weight, while the females of these species appear to weight about 29–34 kg. *H.*

TABLE 6. Body weight estimates and predicted energy expenditure for fossil hominid species

Species	Sex	Weight (kg) <sup>1</sup>	RMR (kcal/d) <sup>2</sup>	TEE1 (kcal/d) <sup>3</sup>	TEE2 (kcal/d) <sup>4</sup>	TEE3 (kcal/d) <sup>5</sup>
<i>A. afarensis</i>	M	44.6	1,208	1,741	1,662	2,408
	F	29.3	882	1,248	1,128	1,319
<i>A. africanus</i>	M	40.8	1,130	1,622	1,549	2,244
	F	30.2	902	1,278	1,136	1,351
<i>A. robustus</i>	M	40.2	1,118	1,603	1,531	2,217
	F	31.9	940	1,335	1,207	1,411
<i>A. boisei</i>	M	48.6	1,288	1,863	1,780	2,577
	F	43.0	986	1,404	1,269	1,484
<i>H. habilis</i>	M	51.6	1,348	1,954	1,866	2,702
	F	31.5	931	1,322	1,195	1,397
<i>H. erectus</i>	M	63.0	1,565	2,289	2,186	3,165
	F	52.3	1,361	1,975	1,785	2,087
<i>H. sapiens</i>	M	65.0	1,602	2,346	2,240	3,244
	F	54.0	1,394	2,026	1,836	2,141

<sup>1</sup> Taken from estimates presented in McHenry (1992b) and Ruff and Walker (1993).

<sup>2</sup> Predicted from the Kleiber equation.

<sup>3</sup> Estimated TEE (kcal/d) based on the general primate predictive equation:  $TEE = 86.0(W_t^{0.792})$ .

<sup>4</sup> Estimated TEE (kcal/d) assuming sex-specific energy budgets similar to a chimpanzee.

<sup>5</sup> Estimated TEE (kcal/d) assuming sex-specific energy budgets similar to contemporary human foragers.

*habilis* appears to be only slightly larger than the australopithecines, with male and female body weights averaging 52 and 32 kg, respectively. It is not until *H. erectus* that we see a substantial increase in hominid body size. For African *H. erectus*, male body size is estimated at 63 kg, while female body size is placed at 52 kg. Body weights for *H. sapiens* are comparable to those of *H. erectus*, averaging 65 and 54 kg for males and females, respectively. Thus, contrary to earlier estimates (e.g., McHenry, 1982) body size does not appear to increase steadily over the course of human evolution. Rather, it seems that hominid body size remained small until 1.7–2.0 mya, when there was an increase with the emergence of *H. erectus* (McHenry, 1992b).

With these data, we can estimate resting energy needs using the Kleiber equation. As shown in Table 6, RMR for females of the four australopithecine species range from 850–1,000 kcal/d while those for males fall between 1,100 and 1,300 kcal/d. Estimates for *H. habilis* are similar to those for the australopithecines (931 and 1,348 kcal/d for females and males, respectively). Those for *H. erectus* and *sapiens*, however, are substantially higher than those for earlier hominids, as female RMRs fall between 1,300 and 1,400 kcal/d, and male RMRs range between 1,500 and 1,600 kcal/d. Thus, since the emergence of the hominid lineage, individual resting metabolic requirements have increased by more than 40%, with much of

this change occurring with the evolution of *Homo erectus*. Increased body size with *H. erectus* was associated with increases in resting metabolic needs of 31% relative to *H. habilis* (16% for males, 46% for females) and 45% relative to *A. africanus* (38% for males; 51% for females).

**Activity patterns and TEE.** Estimating total energy expenditure in early hominids is more problematic because the fossil record provides us with little information for understanding ranging behavior and activity budgets. Consequently, we will estimate TEE using a variety of different assumptions about changes in ranging behavior during human evolution. This approach will allow us to examine how the *interaction* of changes in body size and ranging/foraging patterns contribute to changes in TEE.

Table 6 presents estimates of TEE using three distinct models: (1) a general primate model based on the TEE vs. weight regression presented in equation 5, (2) a chimpanzee model, which assumes that hominid males and females deviate from equation 5 in the same manner as chimpanzees, and (3) a human model, which assumes that hominid males and females deviate from equation 5 in the same manner as contemporary human foragers. The human model consistently provides the highest estimates for TEE, while the chimp model produces the lowest. Estimates from the human model

indicate that male TEE increased from about 2,200–2,400 kcal/d to 3,100–3,200 kcal/d (35–40%) between the early australopithecines (*A. afarensis* and *africanus*) and *H. erectus*, while female TEE increased from 1,300–1,400 kcal/d to 2,000–2,100 kcal/d (50–55%) over the same period.

Using the other two models, the proportional increases are comparable, but the absolute changes are smaller. Both the general primate and chimpanzee models suggest that TEE for hominid males increased from 1,500–1,750 kcal in the early australopithecines to 2,100–2,300 kcal/d in *H. erectus* and *sapiens*. For females, energy needs for the *A. afarensis* and *africanus* are predicted to be 1,100–1,300 kcal/d, while those for *erectus* and *sapiens* span 1,700–2,050 kcal/d.

Archeological and paleoecological data provide some insights into which of the three models may be most appropriate for each of the different hominid species. Recent evidence from the Aramis site in Ethiopia suggests that the earliest australopithecines (those attributed to *A. ramidus*), lived in a relatively wooded environment (White et al., 1994; WoldeGabriel et al., 1994). Similarly, it appears that the habitats of the *A. afarensis* sites of Hadar, Laetoli, and the older levels at the Omo and E. Turkana had large woodland components as well (Boaz, 1988; Harris, 1985). Consequently, it has been argued that the early australopithecines utilized their environment in a way that was similar to a modern hominoid (cf., Tanner, 1981; Stern and Sussman, 1983; Leonard and Hegmon, 1987).

From 2.5 to 1.5 mya, there was a dramatic reduction in forested areas throughout eastern and southern Africa (Behrensmeyer and Cooke, 1985; Vbra, 1985, 1988, 1993). The transition from woodland to open savanna environments in many parts of Africa promoted changes in both the abundance and distribution of food resources (Foley and Lee, 1989). As their habitat became more open and food resources became more patchily distributed, early members of the genus *Homo* may have expanded their home ranges. Based on the evidence from several Oldowan sites, Potts (1988) suggests that by at least 2 mya, hominids had begun to utilize their environment in a manner that

was different from most other primates. He argues that early members of the genus *Homo* foraged over relatively larger areas, and transported food resources back to home bases. This interpretation implies that it was not until the evolution of *Homo* that hominid foraging ranges and activity patterns became more similar to those of modern hunter-gatherers.

These data suggest that the chimpanzee model is most appropriate for the australopithecines, the human model is most reasonable for *H. erectus* and *H. sapiens*, and the intermediate model (i.e., the average of the chimp and human estimates) may be most applicable for *Homo habilis*. Estimates from this "mixed model" approach imply that between the early australopithecines and *H. erectus*, male energy expenditure levels doubled (1,500–1,700 kcal/d to 3,100–3,200 kcal/d), while females levels increased by about 80–85% (1,100–1,200 kcal/d to 2,000–2,200 kcal/d).

Expenditure estimates from the primate, chimpanzee, human, and mixed models are summarized in Figure 5. For each model, the mid-sex TEE value of each species is presented. Using the most conservative estimates (the chimp model), TEE appears to have remained fairly constant within the australopithecine lineage (1,300–1,500 kcal/d), increased slightly with the evolution of *H. habilis* (1,550 kcal/d), and increased more markedly (1,900–2,000 kcal/d) with *H. erectus*. In contrast, the mixed model shows more dramatic increases, from 1,300–1,500 kcal/d in the gracile australopithecines, to 1,400–1,500 kcal/d in the robust australopithecines, to about 1,700–1,800 kcal/d in *H. habilis* and 2,500–2,600 kcal/d in *H. erectus*.

Overall, these models all show that the most marked increase in energy demands likely occurred with the evolution of *H. erectus*. Some of this projected increase directly reflects the larger body mass of *H. erectus* relative to the australopithecines. However, if foraging ranges did expand with early *Homo*, as the archeological evidence seems to suggest, then it is likely that the energy demands of *H. erectus* increased to a much greater extent than can be attributed to body size alone. Indeed, the data presented in Table 6 and Figure 5 indicate that

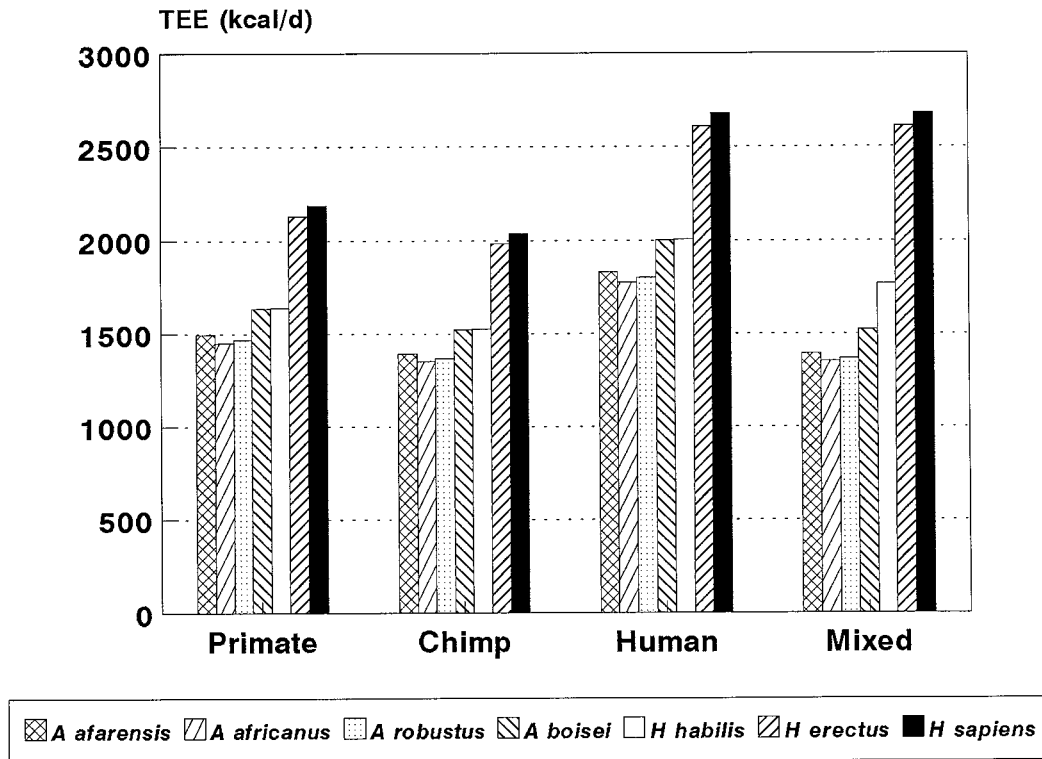


Fig. 5. Four estimates of total energy expenditure (TEE; kcal/d) in early hominid species. All values represent male-female averages. See text for explanation of how the each of the four estimates was derived.

differences in body size likely resulted in a 500–600 kcal increase in *per capita* TEE between *A. africanus* and *H. erectus* (a change of about +40–45%). If there was a shift in ranging behavior as well, as implied by the “mixed” model, the resulting increase in TEE would have been about 1,200 kcal/person/day (+85%), *double* the amount attributable simply to increased size. It thus appears that changes in both size and foraging behavior with *H. erectus* would have had very important energetic consequences.

**Diet and feeding strategies.** Estimates of body size and energy requirements indicate that important changes occurred with the emergence and early evolution of the genus *Homo* (especially *H. erectus*). To understand the significance of these changes for diet and foraging behavior, it is useful to examine them within the context of apparent changes in ecosystem structure and pro-

TABLE 7. Net primary, secondary (herbivore), and tertiary (carnivore) productivity in tropical savanna and woodland ecosystems<sup>1</sup>

Ecosystem	Primary (kcal/m <sup>2</sup> /yr)	Herbivore (kcal/m <sup>2</sup> /yr)	Carnivore (kcal/m <sup>2</sup> /yr)
Forest/woodland	7,200	3.6	0.03
Savanna	4,050	10.1	0.08

<sup>1</sup>Data derived from Begon et al. (1990), Leith (1975), and Heal and McLean (1975).

ductivity during the Plio-Pleistocene in Africa.

Assuming that a moderately productive woodland and an average savanna bracket the types of ecosystems of the earliest australopithecines through the emergence of African *H. erectus*, we can examine how energy availability may have changed over that time. Table 7 presents net primary, secondary (herbivore), and tertiary (carnivore) productivity (kcal/m<sup>2</sup>/yr) for contemporary tropical woodland and savanna ecosystems. Note

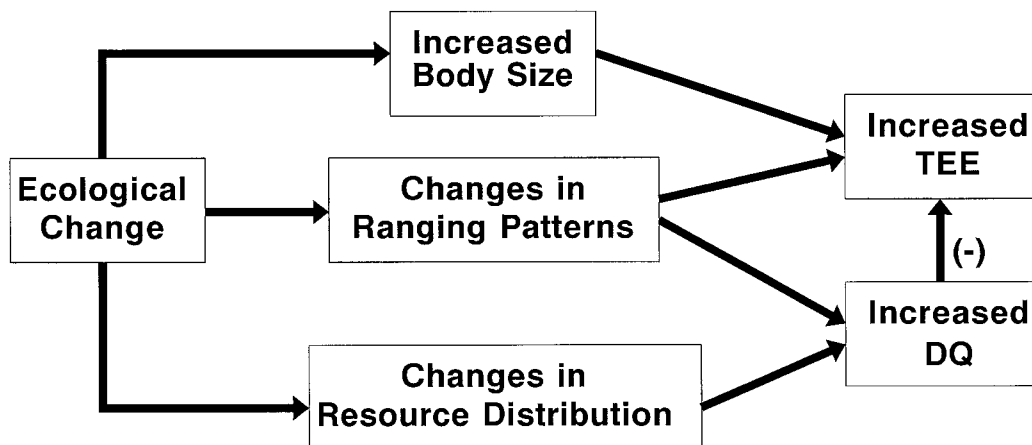


Fig. 6. Flow diagram depicting the hypothesized relationships between changes in ranging behavior, total energy expenditure, and diet quality with the emergence of early *Homo*. Expansion of grasslands in E. and S. Africa likely changed the distribution of food resources and may have necessitated larger foraging

ranges for hominids. The adoption of novel foraging regimes with *H. habilis* and *H. erectus* may have increased dietary quality, which would have been critical for supporting the higher TEE levels associated with larger foraging ranges.

that while the annual primary productivity of the savanna is little more than half that of the woodland (7,200 vs. 4,050 kcal/m<sup>2</sup>), the level of herbivore productivity is nearly three times greater in the savanna (10.1 vs. 3.6 kcal/m<sup>2</sup>). This difference reflects differences in herbivore consumption rates between forest and grassland ecosystems. Because much of the plant production is not available to herbivores in a forest, consumption rates are typically low, about 5% of net primary productivity. In grassland environments, on the other hand, consumption rates may be as high as 50% or more<sup>3</sup>; consequently, a larger share of available energy is transferred to higher trophic levels in savanna ecosystems (Begon et al., 1990; Leith, 1975).

These data then provide quantitative support for the generally held assertion that the amount of energy "on the hoof" increased for hominids in more open environments. Animal foods would have been an attractive resource for early hominids because of their greater caloric density and digestibility relative to plant foods. Meat provides 100–200 kcal of metabolizable energy for 100 g consumed, as compared to 10–20 kcal/100 g for leaves, 50–100 kcal/100 g for fruits (Wu Leung, 1968). Therefore, a hominid with

sufficient technology to utilize additional animal resources could have significantly increased its rates of caloric return. Such an interpretation is consistent with the archaeological evidence which shows animal bone accumulations and improvements in lithic technology at sites of early *Homo* (Leakey, 1971; Bunn and Kroll, 1986; Potts, 1988). Although there is debate over whether this meat was obtained largely through hunting or scavenging (cf., Bunn and Kroll, 1986; Shipman, 1986), it seems clear that these hominids were utilizing substantially more meat than has been observed in comparably sized nonhuman primates (e.g., chimpanzees). The shift away from a diet composed largely of tough and fibrous plant foods is also consistent with the reduction of craniofacial robusticity and posterior tooth size seen with the emergence and early evolution of the genus *Homo* (Wolpoff, 1980).

In short, changing patterns of resource distribution in eastern and southern Africa between 2.5 and 1.5 mya may well have been the impetus for the evolution of an early human-like hunting-gathering strategy with early *Homo*. This new foraging strategy, with greater use of tools, division of labor, and sharing of resources likely would have resulted in increased energy returns and greater diet quality. Moreover, evidence from

<sup>3</sup>In this example, herbivore consumption rates were assumed to be 5% in the forest and 25% in the savanna (after Heal and McLean, 1975).

modern primates indicates that an increase in dietary energy and quality would have been critical for supporting the expansion of ranging behavior and greater daily energy expenditure that were likely associated with the evolution of a human-like hunting and gathering regime. This model linking environmental changes with increases in TEE and DQ is summarized in Figure 6.

### CONCLUSIONS

The study of daily energy demands offers to provide important insights into behavioral and foraging ecology of extant primates and early hominids. Results presented here demonstrate that among living primate species, dietary quality is positively correlated with both day range and relative energy expenditure, implying that more active species consume more energetically dense diets. Human foragers fit this pattern in having high levels of energy expenditure, large foraging ranges and a high quality diet (i.e., relatively large amounts of animal foods). In contrast, species subsisting on poor-quality diets (e.g., howler and colobus monkeys) tend to have small ranges and low TEEs for their size.

In examining the fossil record, it appears that daily energy needs increased substantially in *H. erectus* relative to the earlier australopithecines. This increase reflects the larger body size of the *H. erectus* and possibly increases in foraging range and activity levels. Assuming comparable activity budgets among all early hominids species, estimates of TEE are some 40–45% greater in *H. erectus* than in the australopithecines. If, however, it is assumed that ranging behavior changed from “chimpanzee-like” to “human-like” with the evolution of the genus *Homo*, TEE estimates for *H. erectus* are, on average, 80–85% greater than in the australopithecines. Changing patterns of resource distribution associated with the expansion of African savannas between 2.5 and 1.5 mya likely would have made animal foods a more attractive resource. The resulting higher quality diet may have been critical for supporting increased foraging ranges and higher daily energy requirements that appear to have been associated with the evolution of a human-like hunting and gathering strategy.

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